

ON THE AFFINITIES AND HABITS OF *THYLACOLEO*.

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The nature of few fossil animals has been more discussed than that of the remarkable extinct Australian form to which Owen gave the name of *Thylacoleo carnifex*. Not only has there been considerable difference of opinion as to the affinities of the animal, but its probable habits have been even more debated.

The first important paper on *Thylacoleo* was published by Owen in 1859.* In this paper are described the greater part of the posterior half of the skull, a fragment of the maxilla, and the main part of the ramus of the lower jaw. From the examination of the foramina at the base of the skull, together with one or two other characters, Owen was led to conclude that the remains were those of a Marsupial, while from the characters of the temporal fossæ, occiput, and especially from the rudimentary condition of the molars, together with the enormously large and cutting premolars, which bore a considerable superficial resemblance to those of the cat tribe, he was further led to the conclusion that the form had been a carnivore, and "one of the fellest and most destructive of predatory beasts."† His views of its affinities at this time probably were that it had its nearest relatives in the *Dasyuride*, bearing apparently a somewhat similar relationship to the existing carnivorous forms that the lion does to the dog. At this time there was no evidence as to whether the large tooth in the front of the jaw, indicated only by the socket, was a canine

* On the Fossil Mammals of Australia. Part i. Description of a mutilated Skull of a large Marsupial Carnivore (*Thylacoleo carnifex*, Owen) from a calcareous conglomerate stratum, eighty miles S.W. of Melbourne, Vic. Phil. Trans. Vol. 149, 1859.

† *Loc. cit.* p. 319.

or a terminal incisor, and though Owen inclined to regard it as a canine, he admits the possibility of its being an incisor, in which case he recognised that the affinities would be more with the Diprotodonts, for he adds:—"If, however, this be really the foremost tooth of the jaw it would be one of a pair of terminal incisors according to the marsupial type exhibited by the *Macropodide* and the *Phalangistide*."*

In 1866, through receiving further material from Australia, Owen† was enabled to describe the greater part of the skull and of the lower jaw, and to indicate fully the nature of the dentition. It was now clearly shown that the large anterior teeth were incisors which in Owen's opinion "proved the *Thylacoleo* to be the carnivorous modification of the more common and characteristic type of Australian Marsupials, having the incisors of the lower jaw reduced to a pair of large, more or less procumbent and approximate, conical teeth or 'tusks.'"‡ Not only did the additional evidence confirm him in his opinion that *Thylacoleo* was a carnivore, but he considers that in this extinct form we have "the simplest and most effective dental machinery for predatory life and carnivorous diet known in the Mammalian class. It is the extreme modification, to this end, of the Diprotodont type of Marsupialia."§ Beyond admitting its affinities with the Diprotodonts he does not seem to have regarded it as a near relative of any of the existing groups. But from his statements in the article on Palæontology in the Encyclopædia Britannica, 8th Edition, 1859, he apparently regarded *Thylacoleo* as related to *Plagiaulax*.

In 1868, Flower read a paper before the Geological Society of London—"On the Affinities and probable Habits of the Extinct

* *Loc. cit.* p. 318. [See also a later paper, Vol. 174, Pt. ii. 1883, pp. 576-577.—ED.]

† On the Fossil Mammals of Australia. Part ii. Description of an almost entire Skull of *Thylacoleo carnifex*, Owen, from a fresh-water deposit, Darling Downs, Queensland. Phil. Trans. 1866, clvi. p. 73.

‡ *Loc. cit.* p. 80.

§ *Loc. cit.* p. 81.

Australian Marsupial, *Thylacoleo carnifex*, Owen."* In this paper, while agreeing with Owen's opinion that *Thylacoleo* is more nearly allied to the Diprotodonts than to the existing carnivorous forms, he altogether differs from Owen's conclusion that the animal was a carnivore. While the large premolar had struck Owen as being closely paralleled by the last premolar in the lion, Flower is more impressed by its resemblance to the homologous tooth in the Rat-kangaroo. The latter author considers that it can be "easily shown" "that the resemblance of the great premolar of *Thylacoleo* to the 'carnassial' of the true Carnivora is merely superficial."† "Indeed," he adds, "there is no tooth, either in the upper or lower jaw, of any of the Thylacines, Dasyures, or Opossums, that can be with any reason compared with them [the teeth of *Thylacoleo*]. When, however, we pass to another group of the same sub-class, the Hypsiprymni or Rat-kangaroos, we see at once in the great cutting premolar a miniature of that of *Thylacoleo*."‡ In support of this view he points out the main features of the tooth in the Rat-kangaroos and the marked degree of variability. He then considers the other teeth, and concludes that "in the number and arrangement of these teeth . . . *Thylacoleo* corresponds exactly with the modern families *Macropodidæ* and *Phalangistidæ*, and differs completely from the carnivorous marsupials."§ The remarkable reduction of the true molars, he considers, "is evidently in relation with the excessive development of the great trenchant premolar,"|| and he points out that there is a tendency to reduction of the true molars in the Rat-kangaroos. The small size of the brain cavity and the great development of the temporal ridges he considers to be "probably only a difference of the kind always

* Q.J.G.S. 1868, p. 307.

† *Loc. cit.* p. 309.

‡ *Loc. cit.* p. 310.

§ *Loc. cit.* p. 311.

Loc. cit. p. 311.

observable in comparing large with small species of a natural group."* Having dealt with its affinities, Flower proceeds to consider the probable habits of this animal which Owen had supposed to be a sort of pouched-lion. Towards the solution of this question he propounds the following proposition which he thinks will be generally accepted:—"That if all the known species of a large group of animals with teeth formed on one peculiar type lead lives peaceable and inoffensive to their neighbours, and feed mainly on vegetable substances, the probabilities, in the case of any newly discovered species having teeth constructed on the same general type, are greatly in favour of its having possessed similar habits and been nourished by a corresponding diet."† Assuming this proposition to be correct, he has no difficulty, after having settled its affinities, in concluding that *Thylacoleo* was a vegetable feeder, and he considers that there is no reason why the large premolar should not have been "as well adapted for chopping up succulent roots and vegetables as for dividing the nutritive fibres of animal prey."‡ He also states the food of *Thylacoleo* "may have been some kind of root or bulb; it may have been fruit; it may have been flesh" §; but he does not consider that the organisation of the animal suited it for preying on the large Diprotodonts.

Some years before the publication of Flower's paper, Falconer,|| in dealing with the probable habits of *Plagiaulax*, which Owen had regarded as a carnivorous form, set forth a number of arguments in favour of its being a herbivore, very similar to those which Flower has applied to *Thylacoleo*, so that though Falconer apparently agreed with Owen as to the habits of *Thylacoleo*, his various arguments if applied would more logically make him a supporter of Flower's position.

* *Loc. cit.* p. 311.

† *Loc. cit.* p. 315.

‡ *Loc. cit.* p. 318.

§ *Loc. cit.* p. 318.

|| "On the disputed affinity of the Mammalian Genus, *Plagiaulax*, from the Purbeck Beds." Q.J.G.S. 1862, xviii. p. 384.

Gerard Krefft,* formerly Curator of the Australian Museum, Sydney, published in the same year as Flower dealt with this subject, a short note in the *Annals and Magazine of Natural History*, in which he states his belief that *Thylacoleo* was "not much more carnivorous than the Phalangers of the present time."†

To his various opponents Owen‡ replied in a lengthy paper in the *Philosophical Transactions* for 1871. Flower and Falconer both found their conclusions largely on the fact that a diprotodont dentition is among living Marsupials and in most Eutheria met with only in herbivorous forms; Owen's position on the other hand is mainly founded on Cuvier's principle that the molar teeth always indicate whether an animal has been herbivorous or carnivorous, and he holds that in the teeth of *Thylacoleo* we have "no molar machinery for the mastication of vegetable food, but a maximised modification of the teeth for the division of fleshy fibre, and so much of the tubercular form added for the final crush or squeeze of gristle or other tough part escaping the shears, as exists in the most carnivorous of placental mammals."§ With the view that *Thylacoleo* was a pure carnivore, he holds that all the other parts of the dental set are in complete harmony—the sharp incisors being here constructed "to pierce, retain, and kill," and thus performing the functions of the more usual canines. That a diprotodont dentition can be modified to suit the requirements of a carnivorous animal Owen brings forward quite a series of forms to show. The low position of the condyle and its shape are, he holds, additional evidences in favour of carnivory. Having discussed the various arguments in favour of *Thylacoleo* being a herbivore, he proceeds to deal with the affinities of the form and concludes that it is moderately

* "On the Dentition of *Thylacoleo carnifex*." *Ann. & Mag. Nat. Hist.* 1866, (3), xviii. p. 148.

† *Loc. cit.* p. 149.

‡ On the Fossil Mammals of Australia. Part iv. Dentition and Mandible of *Thylacoleo carnifex*, with remarks on the arguments for its Herbivory. *Phil. Trans.* Vol. 161, 1871, p. 213.

§ *Loc. cit.* p. 228.

nearly allied to *Plagiaulax* and considerably removed from existing Diprotodonts.

In 1872 Krefft* communicated a second short paper to the Annals & Magazine of Natural History, in which he agrees in the main with Flower's position. In this paper he records his opinion "that the animal under discussion is a mixed feeder allied to the phalanger tribe."† But he appears to have been slightly in doubt as to the habits, for he states that "with the true molars reduced to a pair below, one of which is tubercular, and to a single transverse tooth above, the somewhat carnivorous character of the animal becomes manifest;"‡ while further on in the same paper he speaks of *Thylacoleo* as a "certainly harmless creature,"§ and in a paper published a year later,|| he says,— "the view I took first of the herbivorous habits of the 'lion in phalanger hide' was a perfectly correct one."¶

Since then, beyond a short paper by Owen** in 1887, in which he describes the posterior part of a perfect jaw, I am not aware of any special papers having been published on the subject, but numerous short notes have appeared by various scientists in different publications.†† Flower's article on Mammalia in the 9th

* "A Cuvierian Principle in Palæontology tested by evidences of an Extinct Leonine Marsupial (*Thylacoleo carnifex*), by Professor Owen, F.R.S." Reviewed by Gerard Krefft. Ann. & Mag. Nat. Hist. 1872, (4), x, p. 169.

† *Loc. cit.* p. 175. ‡ *Loc. cit.* p. 174. § *Loc. cit.* p. 181.

|| "Australian Natural History." Trans. Roy. Soc. N.S.W. 1873, p. 135.

¶ *Loc. cit.* p. 138.

** "Additional Evidence of the Affinities of the Extinct Marsupial Quadruped, *Thylacoleo carnifex*, Owen." Phil. Trans. 1887, B.

†† [It seems desirable to mention that when this paper was written the author was resident in Namaqualand, Cape Colony, quite out of reach of libraries. Otherwise no doubt some special reference would have been made to two papers by Mr. De Vis, of the Queensland Museum, in which the carnivorous (ossiphagous) character of *Thylacoleo* is upheld ("On Tooth-marked Bones of Extinct Marsupials," P.L.S.N.S.W. 1883, viii. p. 187; and "On a Femur probably of *Thylacoleo*," Proc. Roy. Soc. Queensland, 1886, iii. p. 122). Two later papers by Prof. Owen ("On the Affinities of *Thylacoleo* and on the "Pelvic Characters of *Thylacoleo carnifex*," Phil. Trans. Vol. 174, Part ii. 1880, pp. 575 and 639) have also been inadvertently overlooked.--ED.]

Edition of the Encyclopædia Britannica, 1883, shows that he still maintains his early opinion. And in more recent times Flower's position has received the support of one of our most distinguished palæontologists, Mr. R. Lydekker.*

Whatever difference of opinion may still exist as to the habits of *Thylacoleo* from what is now known of its structure, its affinities can be made out with tolerable certainty. The structure of the lower jaw and the dentition render it manifest that the form is more nearly related to the Phalangers than to any other living group, and there are none of the cranial characters but are quite in harmony with this conclusion. In none of the living Phalangers is there a similar enlargement of the posterior premolar, but in the *Macropodidæ* which have manifestly been an offshoot from the Phalangers, the enlarged premolar has been retained in many of the forms—especially the smaller Rat-kangaroos. About three years ago I discovered in a bone breccia deposit near the Wombeyan Caves, N.S.W., the remains of an interesting little Marsupial, which I described in a paper communicated to this Society, † under the name of *Burramyssparvus*. This little form, which is evidently the representative of a sub-family of the *Phalangeridæ*, and to which the name *Burramyince* may be given, in most of its characters agrees with the Phalangers, but it possesses the greatly enlarged and grooved premolars of the Rat-kangaroos; and it will be observed that not only does it show the evidence of a group which fills the only remaining gap between the Kangaroos and the Phalangers, but as a Phalanger with the posterior premolars enormously enlarged it comes nearer to *Thylacoleo* than does any extinct or living form hitherto discovered.

* Manual of Palæontology by Nicholson & Lydekker, Vol. ii, 1889. Also Royal Natural History, Vol. iii. 1894, p. 264.

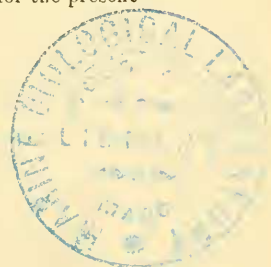
† “On a small fossil (Diprotodont) Marsupial, with large grooved Premolars.” P.L.S.N.S.W. 1895, p. 563. Also “Report on a Bone Breccia Deposit near the Wombeyan Caves, N.S.W.; with Descriptions of some new fossil Marsupials.” P.L.S.N.S.W. 1896, p. 48.

Before, however, discussing the relations and habits of *Thylacoleo* it may be well to make a short digression to consider the origin and probable phylogenetic history of the enlarged premolar as found in *Burrhamys* and carried on into the *Macropodide*. Though grooved premolars occur in the *Plagiulacide* it will be unnecessary at present to discuss that group, as it is certainly not nearly related to the existing Diprotodont Marsupials, and any similar development can only have been due to a parallel development.

Let us imagine a small *Dromicia*-like Phalanger which, from necessity, had to live less exclusively on succulent leaves and other soft substances and had to make up the deficiency with grass. Eucalyptus and other succulent leaves, fruits, and even insects, can be broken and crushed, but grass requires to be cut, and the comparatively feeble and pointed incisors would unaided be unable satisfactorily to finely cut the tougher fibres of the new diet. The sharp-edged premolars would be called in to assist in the dividing process and the increased work given to them would lead to their greater development. It is further not difficult to see the advantage that would result from a serrated edge being acquired, though the exact details by which the serrations would arise could not well, with the meagreness of the data, be more than roughly guessed at. Such a development and specialisation of the posterior premolar would give rise to a form closely resembling *Burrhamys*. In the Macropod line of descendants the arboreal life is more or less completely abandoned, and the whole organisation has been modified to suit a ground life and a diet of grass and other fibrous plants and roots. The lower limbs have become lengthened and strengthened to enable the animals to escape their enemies by flight; and the hallux or "thumb" being a useless encumbrance, no longer required for grasping the boughs, has been early lost. In only one species of the *Macropodide* (*Hypsiprymnodon moschatus*) does the hallux still remain, apparently an ancestral type and one which forms an almost perfect link between the *Burrhamys*-like species and the Rat-kangaroo. The few forms which have returned to an arboreal life, such as

Dendrolagus, cannot regain the lost "thumb," and are at most slightly modified Wallabies. All the known Rat-kangaroos—which are, there is little doubt, the more primitive members of the group*—are of small size, and their dentition is invariably suited to a fibrous vegetable diet, principally of grass. Though in *Burramys* there are but three molars above, and the fourth below rudimentary, there can be no doubt that in closely related forms the normal number was present, and the changes which would be required to give rise to such a dentition as is met with in the Rat-kangaroos from a *Burramys*-like ancestor are very slight. The increased grinding work entailed by the tougher vegetable diet would lead to the retention and greater development of the four molars; and while the large cutting premolars would be also retained and modified slightly to suit the special requirements of the various species, the rudimentary premolars being functionless would become lost. In the further development of the *Macropodidae* which gave rise to the Kangaroos and Wallabies a most interesting change has taken place. Owing to the increase in size of the forms and also to the loose mode of attachment of the jaws to each other, the cutting functions can all be performed by the incisors, and the large premolars which had been functional in the lower forms became much reduced in size, and in the larger species are of so little importance that they are lost shortly after the animal becomes adult without apparently causing any inconvenience. It will thus be seen that there are fairly good reasons for believing that the unusually large development of the last premolar has been brought about in connection with the more

* The position of *Triclis*, De Vis, is uncertain. Lydekker says of it (Palæontology by Nicholson & Lydekker, Vol. ii. p. 1286), "there is a minute tooth behind the lower incisor corresponding to the tooth in the *Phalangeridae*, commonly reckoned as the representative of the canine [2nd incisor—Thomas]." If this observation be correct it is certainly an interesting Phalangeroid character, but De Vis informs me that the dentition in the adult jaw is "I¹; C⁰; P⁴; M^{1, 2, 3, 4}." It will thus for the present be safer to omit consideration of this form.



fibrous vegetable diet partaken of by those descendants from the Phalangers which had more or less abandoned an arboreal life.

Before considering the relations of *Thylacoleo* to this line of forms with the enlarged premolars it will be necessary to look at the much discussed question of the habits of the animal. Owen has pointed out that in the large sharp-pointed incisors, together with the powerful cutting premolars, we have a dental machinery very similar to that found in the cat tribe—the large incisors taking the place of the carnivore canines—“to pierce, retain and kill”; and that such a dental machinery, though well adapted for a carnivorous diet, would be quite unsuitable for any other; and he has further shown that the structure of the jaw and the cranium confirms the conclusion arrived at from a consideration of the dentition. The main argument of Falconer, Flower, Krefft, and Lydekker on the other hand in favour of *Thylacoleo* being a herbivorous form is that practically all known Diprotodont Marsupials are herbivorous, or mainly herbivorous, and that as *Thylacoleo* is a Diprotodont it most probably likewise had mainly a vegetable diet. That this does not unfairly represent the position will be seen from the proposition of Flower's already quoted, and from the following extract from Lydekker* :—“In originally describing this remarkable animal from fragments of jaws containing the fourth premolar, Sir Richard Owen came to the conclusion that the structure of this tooth indicated a carnivorous animal adapted to prey upon the huge Diprotodonts and Nototheres; but the discovery of the complete skull has shown that the animal was more closely allied to the existing Phalangers, and that it could not have possessed the destructive habits attributed to it by its describer, though it is quite possible that its diet may have included the smaller mammals, birds, and eggs.” Apart from the exception which may be taken to the reasoning involved in this statement, it in my opinion somewhat misrepresents Owen's

* Manual of Palæontology by Nicholson & Lydekker, 3rd Ed. Vol. ii. 1889, p. 1285.

position, for even in his very first paper he admits the possibility of *Thylacoleo* being allied to the Phalangers, and when more perfect specimens were discovered which proved it to be so, it in no way altered his opinion that *Thylacoleo* was nevertheless a carnivorous animal.

Let us consider, however, whether there is really such a great improbability, as Falconer and Flower seem to think, in a Diprotodont Marsupial becoming a carnivore, that *Thylacoleo* may with such confidence be referred to the vegetable feeders. The question divides itself into two—(1) whether the diprotodont dentition can be modified to suit a carnivorous diet, and (2) whether in a group of animals in a which a certain type of dentition is universal and the habits apparently uniform, an aberrant form may be met with which puts the same type of dentition to quite a different use.

Though Falconer and Flower have inclined to the view that a carnivorous animal to be able satisfactorily to kill its prey requires canines separated by a row of incisors, the large series of forms given by Owen which are carnivorous and yet have the functions of the canines entirely performed by large incisors sufficiently answers the first question. Flower, however, qualifies his statement by defining a "true predaceous carnivorous animal" as "one which kills and eats creatures at all comparable to itself in bulk and capable of making any effectual resistance."* Were this to be accepted as the definition of a carnivorous animal it would rather complicate matters, for the fish-eating Seals would have to be excluded, and so also would many of our most typical carnivores which habitually feed on small forms. There is no doubt that Owen is right in regarding the Hedgehog as more or less a carnivorous form whose organisation is sufficiently adapted to enable it to kill and eat young rabbits, and if we can thus have a diprotodont dentition which can be satisfactorily used in the killing and eating of small animals all our knowledge of the working of Nature would lead us to believe that she could in an

* *Loc. cit.* p. 317.

animal which had become exclusively carnivorous perfect the same type of dentition for an exclusively carnivorous diet.

The second question arises out of Flower's proposition already quoted. In considering it there is one important fact that must not be overlooked, namely, that while among large herbivorous animals many parts of the organisation become so highly specialised to suit the vegetable diet that it would be impossible for the animal to alter its diet very materially and thrive, in small animals the specialisation is much less marked, and a considerable variety of diet is possible. Thus, while it would be impossible for an ox or a kangaroo to become a carnivorous animal, many of the smaller Rodents and some of the small Phalangers which are normally herbivorous occasionally take to eating flesh, and a number of the small Phalangers are partly insectivorous. The Bandicoots afford a well known instance of a group of animals which are partly herbivorous and partly insectivorous; and among the Insectivora other instances occur. *Macroscelides*, the Elephant-shrew, has a jaw which judging by analogy would certainly be referred to a herbivorous form and the molar teeth would seem to be quite in harmony with this determination, and yet though *Macroscelides* is largely a vegetable feeder I have found in the stomach abundant remains of ants and even of fairly large beetles. But perhaps in no Order is there a more remarkable instance of change of diet than in the Chiroptera. Had *Pteropus* been first discovered as a fossil it would, according to the reasoning of Falconer and Flower, almost certainly have been regarded as an insectivorous or carnivorous form. Here we have a form, it would be held, closely allied to the insectivorous bats and having a very similar type of dentition—large canines separated by a row of small incisors—almost exactly as in the normal carnivorous types and quite unlike that found in the normal vegetable feeders, and the conclusion would be arrived at that *Pteropus* was either an insectivore or a carnivore, but most probably not a vegetable feeder. And yet the conclusion would be wrong. But were Cuvier's principle taken as the guide only a correct conclusion could be arrived at.

It is remarkable that the structure of the molars in *Thylacoleo* has been so lightly passed over by those supporting the herbivorous hypothesis. Flower and Lydekker evidently consider that the molars have been reduced through their functions being taken up by the large premolars. But could the large premolars take up the molar function—could they grind? Even those who favour the idea of *Thylacoleo* being a vegetable feeder admit that the premolars were cutting teeth, and the difficulty of imagining a herbivorous animal without grinders is got over by supposing that its food was of a soft or succulent nature. Flower thinks the food “may have been some kind of root or bulb; it may have been fruit,” he says, or “it may have been flesh”; while Lydekker, though he believes the main diet to have been of a vegetable nature, thinks it may have included “the smaller mammals, birds and eggs.” Though so many alternative diets have been suggested as possible, Flower presumes with Lydekker that *Thylacoleo* was a vegetable feeder, and I take it that neither believes *Thylacoleo* to have been a regular omnivorous animal feeding regularly on succulent roots, fruits, mammals, birds and eggs, but rather that succulent vegetables and fruit formed the staple diet and that animal food was partaken of only exceptionally.

For *Thylacoleo* to have lived on succulent roots and bulbs, the vegetation of the portion of Australia which it inhabited must have been very different in character from that now prevailing; and this is what Flower assumes. Though, however, this is possible, it must be admitted that as yet there is no palæontological evidence of any such radical change in the flora as will parallel that in the fauna.

But there are insuperable difficulties in the way of considering *Thylacoleo* a bulb- or fruit-eater. With its remarkable dentition the animal would be unable to do more than slice its fruits and vegetables even if it could have procured both in abundance, which is so exceedingly improbable. Now, it can hardly be denied that no mammal would be able to digest vegetables, bulbs

or fruits swallowed in slices, unless perhaps when the fruits were drop ripe. But apart from the difficulty that fruits are only ripe at one or occasionally at two seasons of the year, unless we are also to assume the very improbable condition of there being no parrots, parrakeets, cockatoos or flying foxes, there would be very little chance of the fruit ever being allowed to become drop ripe. With succulent roots and bulbs the same difficulty arises as with the fruits, that even the most succulent, if we could suppose them digestible in slices, cannot be had in a succulent condition all the year round.

With regard to the suggestion that "small mammals, birds, and eggs" may have formed part of the diet, it depends considerably on what size of birds and mammals is meant, whether such can be regarded as possible. There are no birds in Australia which *Thylacoleo* would have been at all likely to capture, except perhaps the large flightless Emus and Cassowaries, and even if other small flightless sorts existed, which is exceedingly improbable with Thylacines, Sarcophiles and Dasyures prowling about, they could not have been numerous or lasted long; while if the Emus and other allied forms were eaten surely *Thylacoleo* must be regarded as a carnivorous animal. As for mammals, we are fortunately not in ignorance of the smaller sorts that were contemporaries of the *Thylacoleo*, and we find that though many of the species were different the general character of the fauna differed but little from that found to-day. Ring-tailed and Dormouse Phalangers were common, as was also a small form allied to the flying Phalanger; while of the forms frequenting the ground the commonest were Rat-kangaroos, Bandicoots and Rats; and the only other small Mammal that was common was the small pouched-mouse. Whatever were the habits of *Thylacoleo*, it may be regarded as practically certain that it could not have caught any of the arboreal forms, and of the ground-living small mammals the Bandicoots alone might possibly have been captured. But then only an animal that was a regular carnivore would be likely to kill or able to devour a Bandicoot. The close resemblance of the general character of the smaller fauna to that present to-day

would lead us, moreover, to believe that there has probably been no great change in the flora.

It is probably, however, unnecessary to discuss further what food *Thylacoleo* could possibly have obtained, when we have, as I hold with Owen, the most satisfactory proof from its anatomical structure as to what food it did obtain. It must be admitted that *Thylacoleo* had enormous temporal muscles, and it is perfectly certain that such muscles would not have been developed unless the animal required them. For what could such powerful muscles be required? Most certainly not for slicing fruits or succulent roots and bulbs, nor would they be required even for the slicing of fleshy fibres. Temporal muscles are chiefly used apparently for closing the jaws more or less forcibly from the open position, while for the more complicated movements of mastication it is the masseter and pterygoid muscles that are chiefly used. Hence in all carnivorous animals the temporals are largely developed and the masseters more feebly, because the killing process requires a very forcible closing of the jaws, and the work to be done by the premolars and molars is comparatively little. In herbivorous animals the conditions are reversed. The jaws are here rarely required to be opened widely or to be closed with any great force, while a very large amount of grinding work has to be done, hence the temporals are rarely much larger than the masseters and often very much smaller. When we look at *Thylacoleo* we find not only the enormous temporals and only moderate masseters, but everything else about the skull seems to be built on carnivorous lines. Owen has shown the wonderful similarity which exists between the molar machinery in *Thylacoleo* and the lion, and it is hard to conceive as possible any other cause giving rise to such a specialisation in *Thylacoleo* than that which led to a similar specialisation in the cat tribe. Another most striking feature is to be seen in the condition of the incisors. Leaving out of consideration the mode of implantation and structure of the teeth—both confirmatory of the carnivorous hypothesis—there is one point which appears to me absolutely conclusive on the subject. Unless Owen's figures are altogether

unreliable, the lower incisors are quite unlike those of the herbivorous Diprotodonts. In such typical forms as the Wombat, the Koala, the Kangaroo, and the Phalanger, though there are different modifications of the arrangement, we have the lower incisors meeting the upper and forming with them an instrument for biting through a moderately tough fibrous tissue, and even in the very small Diprotodonts, so far as I am aware, the lower incisors always meet and work against the upper. But in *Thylacoleo* we have powerful pointed incisors which do not meet, but overlap. Though technically incisors they are not intended to incise, but to pierce and tear. Such powerful pointed and overlapping teeth, though easily explained on the theory that they were intended to kill and tear animal prey, were never surely provided merely to pierce succulent vegetables or ripe fruit. It might of course be argued that the incisors were used as weapons of defence, as apparently are the canines in the Baboon; but against this idea is the objection that the incisors were put to some use which wore them down and blunted them more rapidly than would be the case if they were chiefly used on the rare occasions when the animal had to defend itself, and furthermore were such the case the temporals would not require to be greatly developed.

There is thus, in my opinion, no other conclusion tenable than that *Thylacoleo* was a purely carnivorous animal and one which would be quite able to, and probably did, kill animals as large as or larger than itself.

Let us now consider how such a huge carnivorous animal might be developed from an herbivorous Diprotodont Phalanger. Though *Burramys* comes nearer to *Thylacoleo* than does any other known form, it could not itself have been a direct ancestor for the following reasons. In the masseteric fossa of *Thylacoleo* is a small foramen which opens through to the inner side of the jaw. In most of the living Phalangers this is lost, though it is still retained in *Petaurus*, and becomes enormously enlarged in the *Macropodide*. In *Burramys* it is also lost, and it seems very improbable that when once lost it could be reproduced in a descendant.

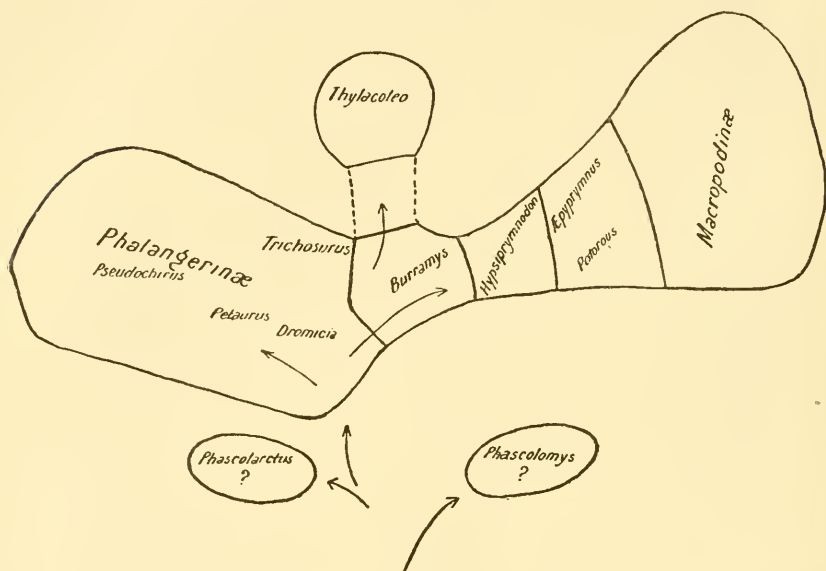
Also in *Burramys* is lost the upper p^1 which is retained in *Thylacoleo*. Still *Burramys* is probably very closely allied to the small Phalanger from which *Thylacoleo* is descended.

As already shown, small mammals which are normally herbivorous very frequently are partly insectivorous, and the type of dentition in *Burramys* is not more typically herbivorous than that in *Macroselides*. Hence there is reason to suppose that the *Burramys*-like ancestor of *Thylacoleo* not improbably varied its herbivorous diet by the addition of insects; as we know the living Phalangers most nearly allied to *Burramys* do to a considerable extent. Such a slight modification of the diet would probably afford the starting point for the new line by which *Thylacoleo* arose. From an animal occasionally partaking of insects it is not difficult to derive one more or less habitually insectivorous. In such a form, the following changes would probably be found. The anterior incisors would be strengthened and become less procumbent. The large premolars would probably be but little altered, being as well suited for the new as for the old function, while the molars would become markedly cuspid. The jaw would be shortened and strengthened; and we should have a condition not very dissimilar to that found in the larger Shrews, where a diprotodont type of dentition becomes specialised to an insectivorous life. From such a shrew-like form it would not be difficult to derive a larger animal, which would, like the diprotodont Hedgehog, be more or less carnivorous; and in such a type, as the carnivorous habits became more developed, the characteristic features of *Thylacoleo* would soon arise. The jaw would become gradually more powerful, the temporal muscles greatly enlarged, and the whole face broadened and shortened to bring the piercing teeth nearer the pulling force. The great premolar would become more powerful and more specialised for cutting flesh, while the molars, being but little required, would gradually become reduced.

All that would thus be required to bridge over the gap between the more or less herbivorous *Burramyinae* and the carnivorous

Thylacoleo would be a group of probably small insectivorous forms.

In the subjoined scheme an endeavour is made to illustrate the probable phylogenetic relationships of the Diprotodont Marsupials. The exact positions of *Phascolarctus* and *Phascolomys* are left as doubtful, and *Cenolestes* has been omitted, as I consider the evidence which would place it with the Australian Diprotodonts not sufficiently strong, and in any case it is evidently not a near ally of any of the Australian forms.



I am much indebted to my father, Mr. John Broom, for his assistance in copying for me papers which I could not otherwise at present have had an opportunity of seeing.

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